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# EFFECTS OF NEST PREDATION AND BROOD PARASITISM ON POPULATION VIABILITY OF WILSON'S WARBLERS IN COASTAL CALIFORNIA

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ABSTRACT.—We studied the consequences of nest predation and brood parasitism on a population of Wilson's Warblers (*Wilsonia pusilla*) breeding in coastal riparian woodlands in northern California. We monitored 90 warbler nests from 1997 to 2000; only 16 of these produced Wilson's Warbler young. Of 74 failed nests, 73% (54/74) failed due to nest predation. Overall, 33% (30/90) of the nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Nest success, as calculated by the Mayfield method, was 0.085 and notably lower than values reported for other warbler species. We used a simple demographic population model—under scenarios of high, average, and low productivity and survival—to evaluate the viability of this population and found it to be at risk of local extirpation without immigration. This was due to the combined effects of high levels of nest predation and the impacts of brood parasitism. *Received 16 June 2003, accepted 6 April 2004.*

Across their range, breeding populations of Wilson's Warbler (*Wilsonia pusilla*) have been declining at both regional and local scales over the past few decades (Ammon and Gilbert 1999, Sauer et al. 2001). According to Breeding Bird Survey data, Wilson's Warblers across the North American continent have been declining on average 2.0% per year during the period 1980 to 2000, and populations along the Pacific coast have been declining on average 1.8% per year over the same time period (Sauer et al. 2001). In contrast, data from a single site in coastal California indicate that the breeding population there is stable (Chase et al. 1997).

Population declines in breeding songbirds have been attributed to a variety of factors, including, but not limited to, loss, degradation, and fragmentation of habitat and associated factors that affect reproductive success and survival. There is evidence that the Wilson's Warbler population in coastal California is regulated primarily by breeding productivity (Chase et al. 1997); however, the factors that limit productivity are unknown. The leading causes of low reproductive success in songbirds are nest predation by vertebrate predators and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Brittingham and Temple 1983; Martin 1992a, 1992b). High levels of nest predation and brood parasitism have been implicated in the decline of many songbird populations by directly affecting productivity and, ultimately, population dynamics (e.g., Pease and Grzybowski 1995).

While there have been few studies published documenting the breeding ecology and life history characteristics of western populations of Wilson's Warbler (Stewart 1973, Stewart et al. 1977, Ammon and Gilbert 1999), little work has been done to explore causes of recent declines and, more specifically, factors limiting reproductive success. Population declines in the past have been attributed to loss and degradation of riparian breeding habitat (Ammon and Gilbert 1999). However, few estimates of reproductive success exist and, to our knowledge, no Mayfield (1975) estimates of nest success have been reported. There are even fewer accounts of cowbird parasitism and its effects on reproductive success of Wilson's Warblers.

In this study, we report on the breeding biology and population viability of a coastal population of Wilson's Warblers breeding in Marin County, California. Our objectives were to (1) examine the effects of cowbird parasitism and nest predation on warbler reproductive success, and (2) develop a simple demographic population model to assess the viability of this local population.

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## METHODS

*Study areas.*—Our study was conducted in the Golden Gate National Recreation Area (GGNRA) in coastal Marin County, California, just north of the San Francisco Bay area. Fieldwork occurred from mid-April to early August 1997 to 2000 along two riparian woodlands, Lagunitas Creek (38° 02′ N, 122° 45′ W) and Redwood Creek (37° 51′ N, 122° 34′ W). The Lagunitas Creek site contained two plots and the Redwood Creek site three, including Muir Beach. Nest monitoring at Muir Beach was conducted only from 1997 to 1999. Each study plot was approximately 3.6 ha in size.

All study sites were similar in vegetation type and typical of riparian communities in the surrounding area. Red alder (*Alnus rubra*) and willow (*Salix* spp.) dominated the sites with lesser amounts of box elder (*Acer negundo*), California bay (*Umbellularia californica*), California buckeye (*Aesculus californica*), and coast live oak (*Quercus agrifolia*). Understory species consisted primarily of California blackberry (*Rubus ursinus*), Himilayan blackberry (*R. discolor*), poison oak (*Toxicodendron diversilobum*), and fern species.

The areas surrounding the study sites were largely oak-bay woodlands and coastal scrub. At Lagunitas Creek, there was light livestock grazing in fields adjacent to the creek and our plots. We chose to treat the Muir Beach plot separately (even though it is part of Redwood Creek) because (1) it is divided by a road; (2) there is a residential community (~150 homes), small horse stable, and a tavern immediately adjacent; (3) there is a public picnic area and 175-car parking lot within and adjacent; (4) it is a heavily used recreational area with over 400,000 visitors per year (National Park Service unpubl. data); and (5) it is the only plot where unsupervised domestic dogs (*Canis domesticus*) and cats (*Felis domesticus*) were seen.

*Nest searching and monitoring.*—Wilson's Warbler nests were located and monitored using guidelines described by Martin and Geupel (1993). We located nests by observing parental behavior and systematically searching the vegetation. Nests were monitored every 1–4 days until nest failure or fledging. A nest was considered successful if it fledged at least one warbler young. Fledging was assigned based on the condition of the nest (e.g., matted rim and/or fecal matter and no signs of depredation, stage of the nesting cycle), and/or evidence of fledglings within close proximity of the nest near the expected fledging date. We considered a nest to have failed if it was abandoned or depredated (disappearance of nest contents) prior to the expected fledging date.

Nests were considered parasitized if at any stage in the nesting cycle they contained a cowbird egg or nestling. We considered nests to have failed from cowbird parasitism if only cowbird eggs or nestlings were observed in the nest during all observations, nests were abandoned during egg laying and cowbird eggs were present, or if only cowbird eggs or nestlings were present in the nest after warbler eggs or young were observed. Parasitized nests were considered successful if warbler young fledged from the nest.

*Reproductive success.*—Nest survival probabilities were calculated using the Mayfield (1975) method with the standard error estimator developed by Johnson (1979). The Mayfield method is based on nest losses divided by the total number of days nests were observed and, thus, at risk of failure. Survival probabilities were calculated for each stage of nesting (egg laying, incubation, and nestling) and for the entire nesting period. Estimates were based on a 26-day nesting period (4 egg-laying days, 12 incubation days, and 10 nestling days) as determined by our nest monitoring data. When calculating "exposure" days (the total number of observation days) for nests with known fates, we used the midpoint between the last observed active date and the first observed inactive date; for nests with unknown fates, the last active date was used for counting exposure days (Last-Active B method in Manolis et al. 2000). We compared differences in nest success probabilities among nesting stages, study sites, and between parasitized and unparasitized nests with Program CONTRAST (Sauer and Williams 1989).

We also calculated the following components of reproductive success: clutch size, clutch-initiation date, hatching success, nestling number, fledging success, and fledgling number. These were calculated for both cowbirds and warblers separately, with the exception of clutch initiation. Clutch size was based on the maximum number of eggs present throughout egg laying. Clutch-initiation dates were estimated based on the first egg laid for a nesting attempt or backdated to calculate when the first egg was laid. Hatching and fledging success were defined as the total number of nestlings and fledglings, respectively, divided by clutch size. The maximum number of young observed between hatching and fledging was the nestling number. Fledgling number was based on the number of nestlings seen during the last nest check prior to the estimated fledging date for successful nests. Comparisons between parasitized and unparasitized nests were made for all components of reproductive success.

*Population trajectory.*—To evaluate population viability, we developed a simple demographic population model following Pulliam (1988) and Donovan et al. (1995). We calculated lambda ($\lambda$) values using the following equation:

$$\lambda = P_A + P_J B$$

where $\lambda$ is the finite rate of increase, $P_A$ represents adult survival, $P_J$ represents juvenile survival from fledging to the first breeding season, and B is a measure of productivity representing the number of female offspring produced per year. This last component is composed of three sub-components: the number of nesting attempts $\times$ probability a nesting attempt is successful $\times$ number of female young produced per successful nest; the second sub-component incorporates our Mayfield estimates of nest success. $P_J B$ is a measure of recruitment rate based on the number of new female recruits produced per year.

Under this model, which calculates a finite (annual) rate of increase, the population is considered a sink ($\lambda < 1$) if juvenile recruitment is less than adult mortality. Conversely, if juvenile recruitment (i.e., $P_J B$) is greater than adult mortality it is considered a source ($\lambda > 1$), and if the two are equivalent the population is stable ($\lambda = 1$; Pulliam 1988). For our calculations, we used $P_A = 0.503$ ($\pm$ 0.035 SE, 95% CI = 0.435–0.571), the adult survival estimate from coastal Marin County (Chase et al. 1997). Because direct estimates of juvenile survival are largely unknown (Gardali et al. 2003), we used a conservative estimate of juvenile survival and assumed it was 70% that of adults (0.352; Powell et al. 1999, Perkins and Vickery 2001). Based on our field data, the number of female offspring per successful nest was 1.7. The formula was evaluated using two, three, and four nesting attempts due to the variability of the number of nesting attempts per season across the warblers' range (Ammon and Gilbert 1999). Additionally, we used our overall nest survival estimate and its 95% confidence interval, and juvenile and adult annual survival to evaluate the population under the observed average, best-, and worst-case scenarios.

*Statistical analysis.*—Nominal logistic regression was used to test for differences in predation and parasitism frequency between sites (Nur et al. 1999). Comparisons of predation rates and nest abandonment between parasitized and unparasitized nests were made using the Pearson chi-square test. We used ordinal logistic regression to determine whether clutch size, hatching success, nestling number, fledging success, and fledgling number were significantly different between parasitized and unparasitized nests. Due to small sample size, data were combined across years and we excluded those nests that were abandoned or depredated prior to the end of egg laying ($n$ = 14). All statistical analyses were performed using JMP software (Sall and Lehman 1996) and means are presented as $\pm$ SE.

## RESULTS

We located and monitored 90 Wilson's Warbler nests over the course of our study. The earliest nest initiation date (first egg laid) was 17 April, and the last was 10 July. Most nests (68%) were built in blackberry shrubs, 18% in ferns, and 12% in eight other plant species. Mean nest height was 50.4 $\pm$ 2.5 cm. Only 16 nests were successful (18%) and 74 (82%) failed to produce young (Table 1).

*Causes of nest failure.*—Nest predation was responsible for more nest failures than failure caused by cowbird parasitism, 73.0% (54/74) versus 13.5% (10/74), respectively. Of 54 depredated nests, 48 were completely depredated, resulting in the loss of the entire clutch or brood, and 6 were partially depredated and subsequently abandoned. The remaining nests were abandoned due to unknown causes ($n$ = 6), failed due to weather ($n$ = 3), or were accidentally destroyed ($n$ = 1). Of the 10 nests

TABLE 1. Nest outcome and causes of failure for Wilson's Warblers breeding in coastal Marin County, California, 1997–2000. BHCO refers to Brown-headed Cowbird parasitism.

| | All nests | Parasitized nests | Unparasitized nests |
|---|---|---|---|
| Nest outcome | | | |
| Total number of nests | 90 | 30 | 60 |
| Successful[a] | 16 | 1 | 15 |
| Unsuccessful | 74 | 29 | 45 |
| Percent successful | 18% | 3% | 25% |
| Causes of nest failure | | | |
| Depredated[b] | 54 | 18 | 36 |
| BHCO[c] | 10 | 10 | — |
| Abandoned (unknown) | 6 | — | 6 |
| Abandoned (weather) | 3 | 1 | 2 |
| Abandoned (other) | 1 | — | 1 |

[a] Nests from which at least one warbler fledged.
[b] Includes four nest failures due to parasitism and subsequent depredation.
[c] Includes four nests fledging BHCO, four lost to predation, and two abandoned.

that failed due to cowbird parasitism, four fledged cowbird young, four were subsequently depredated, and two were abandoned (Table 1).

Nest predation differed among sites for all years combined ($\chi^2$ = 6.58, df = 2, $P$ = 0.043). Predation rates were highest at Muir Beach (91.7%), and lower at Lagunitas Creek (54.5%) and Redwood Creek (61.8%; Table 2). The frequency of predation did not differ between parasitized (73%) and unparasitized (60%) nests ($\chi^2$ = 1.55, df = 1, $P$ = 0.21). Likewise, there was no difference in the frequency of nest abandonment for parasitized (25%) and unparasitized (75%) nests ($\chi^2$ = 0.27, df = 1, $P$ = 0.60).

*Brood parasitism.*—Cowbirds parasitized 33.3% (30/90) of all nests, 3% (1/30) of which were successful, as compared to 25% (15/60) of unparasitized nests. The frequency of parasitism (all years combined) was greater at Muir Beach (83.3%) than at Lagunitas Creek (25.0%) and Redwood Creek (26.5%; $\chi^2$ = 14.97, df = 2, $P$ < 0.001; Table 2). Of the 30 parasitized nests, 26 contained one cowbird egg and 4 had two cowbird eggs. The mean number of cowbird eggs and nestlings per parasitized nest was 1.16 ± 0.07 and 0.77 ± 0.12, respectively (Table 3). At least one cowbird fledged from each of four parasitized nests, and two cowbirds fledged from one nest, for an overall mean of 0.22 ± 0.10 cowbirds fledged per parasitized nest (Table 3). Warbler young fledged from only one parasitized nest. An inactive nest was parasitized after being depredated.

Clutches in parasitized nests contained fewer warbler eggs (1.52 fewer) than unparasitized nests ($\chi^2$ = 43.13, df = 1, $P$ < 0.001; Table 3). Moreover, the percent of warbler eggs that hatched was lower in parasitized nests (35.7%) than in unparasitized nests (63.8%; $\chi^2$ = 5.55, df = 1, $P$ = 0.019; Table 3) and we found fewer warbler nestlings in

TABLE 2. Frequency of nest predation and cowbird parasitism observed in Wilson's Warblers at three sites in coastal Marin County, California, 1997–2000.

| Site | Nest predation | | Parasitism | |
|---|---|---|---|---|
| | % | $n$ | % | $n$ |
| Lagunitas Creek ($n$ = 44) | 54.5 | 24 | 25.0 | 11 |
| Muir Beach ($n$ = 12) | 91.7 | 11 | 83.3 | 10 |
| Redwood Creek ($n$ = 34) | 61.8 | 21 | 26.5 | 9 |
| All sites ($n$ = 90) | 62.2 | 56 | 33.3 | 30 |

TABLE 3. Five estimates of reproductive success for parasitized and unparasitized Wilson's Warbler nests (mean ± SE), coastal Marin County, California, 1997–2000.

| | Wilson's Warbler | | | |
|---|---|---|---|---|
| | Parasitized nests | Unparasitized nests | Combined | Cowbird |
| Clutch size | 1.96 ± 0.16 | 3.48 ± 0.12 | 2.92 ± 0.13 | 1.16 ± 0.07 |
| Hatching success[a] | 0.36 ± 0.09 | 0.64 ± 0.07 | 0.53 ± 0.06 | 0.64 ± 0.09 |
| Number of nestlings | 0.71 ± 0.19 | 2.31 ± 0.26 | 1.72 ± 0.20 | 0.77 ± 0.12 |
| Fledging success[b] | 0.04 ± 0.04 | 0.28 ± 0.06 | 0.19 ± 0.04 | 0.18 ± 0.08 |
| Number of fledglings | 0.11 ± 0.11 | 1.06 ± 0.25 | 0.71 ± 0.17 | 0.22 ± 0.10 |

[a] Hatching success: total number of nestlings/clutch size.
[b] Fledging success: total number of fledglings/clutch size.

TABLE 4. Daily survival and total nest success (Mayfield 1975) for Wilson's Warblers breeding in riparian woodlands, coastal Marin County, California, 1997–2000.

| | Number of nests | Exposure days | Losses | Daily survival (SE, 95% CI) | Nest success (95% CI) |
|---|---|---|---|---|---|
| Lagunitas Creek | 44 | 436 | 30 | 0.931 (0.012, 0.907–0.955) | 0.157 (0.080–0.302) |
| Muir Beach | 12 | 95 | 12 | 0.874 (0.034, 0.807–0.940) | 0.030 (0.004–0.203) |
| Redwood Creek | 34 | 219 | 24 | 0.890 (0.021, 0.859–0.932) | 0.049 (0.014–0.159) |
| All sites | 90 | 731 | 66 | 0.910 (0.011, 0.889–0.930) | 0.085 (0.047–0.154) |

parasitized nests ($\chi^2$ = 14.76, df = 1, $P$ = 0.001). Similarly, fledging success differed between parasitized (3.6%) and unparasitized (27.6%) nests ($\chi^2$ = 8.79, df = 1, $P$ = 0.003; Table 3) and parasitized nests fledged fewer warbler young than unparasitized nests ($\chi^2$ = 9.27, df = 1, $P$ = 0.002). Parasitized and unparasitized nests averaged 0.71 ± 0.19 and 2.31 ± 0.26 nestlings, respectively.

*Daily survival and nest success.*—The Mayfield (1975) estimate of nest success was 8.5% (95% CI = 0.047–0.154; Table 4). Differences among sites in daily survival rates were marginally significant ($\chi^2$ = 4.72, df = 2, $P$ = 0.094; Table 4). Daily survival rates of parasitized and unparasitized nests did not differ ($\chi^2$ = 1.54, df = 1, $P$ = 0.21). Daily survival was lowest during the nestling stage (0.87 ± 0.022), and slightly greater during egg laying (0.93 ± 0.023) and incubation (0.93 ± 0.013; $\chi^2$ = 5.88, df = 2, $P$ = 0.053).

*Population trajectory.*—The demographic population model suggests that this population of Wilson's Warbler is not self-sustaining in the absence of immigration from other populations. We used a value of 1.7 female offspring per successful nest (based on our field data) and evaluated the model under a variety of scenarios. Using conservative estimates of survival and productivity and two nesting attempts, $\lambda$ = 0.46 (Table 5). When intermediate estimates of survival and productivity for birds attempting three nests per season were used, $\lambda$ = 0.62 (Table 5). Under the best-case scenario (high survival and productivity, four nesting attempts per season), $\lambda$ = 0.98 and approaches the value (1) required for a stable population.

## DISCUSSION

Nest success in this study was extremely low. The proportion of successful nests (0.18) was slightly greater than that reported from inner-coastal California (0.16) and far lower than eight other estimates (0.33–0.93; summarized by Ammon and Gilbert 1999).

Since no Mayfield (1975) estimates of nest survival exist for the Wilson's Warbler, we were unable to compare our survival estimates to those of previous studies. While estimates of nest success may be variable across habitat types, years, and between species, our estimates were notably lower than those reported for other warbler species. For example, May-

TABLE 5. Lambda values (finite rate of increase) for population models using mean and 95% confidence intervals for survival and productivity (i.e., low, mean, and high productivity and survival) with two, three, and four nesting attempts for Wilson's Warbler, coastal Marin County, California, 1997–2000. Number of female offspring/successful nest set at 1.7 (see text).

| Number of nesting attempts | Low productivity[a] (lower CI) | | | Mean productivity[b] | | | High productivity[c] (upper CI) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 2 | 3 | 4 | 2 | 3 | 4 |
| Low survival[d] (lower CI) | 0.46 | 0.47 | 0.49 | 0.50 | 0.53 | 0.57 | 0.59 | 0.67 | 0.75 |
| Mean survival[e] | 0.53 | 0.55 | 0.56 | 0.58 | 0.62 | 0.66 | 0.68 | 0.77 | 0.87 |
| High survival[f] (upper CI) | 0.60 | 0.62 | 0.64 | 0.66 | 0.70 | 0.75 | 0.78 | 0.88 | 0.98 |

[a] Low productivity: Mayfield success = 0.047.
[b] Mean productivity. Mayfield success = 0.085.
[c] High productivity: Mayfield success: 0.154
[d] Adult survival = 0.435, juvenile survival = 0.305.
[e] Adult survival = 0.503, juvenile survival = 0.352
[f] Adult survival = 0.571, juvenile survival = 0.400.

field (1975) estimates for the Worm-eating Warbler (*Helmitheros vermivorus*) range from 0.37 to 0.50 in Virginia (Dececco et al. 2000), 0.44 for the Hooded Warbler (*Wilsonia citrina*) in South Carolina (Moorman et al. 2002), and 0.50 for Orange-crowned Warbler (*Vermivora celata*) and 0.58 for Virginia's Warbler (*V. virginiae*) in Arizona (Martin 1992a). The lowest estimate for any warbler (summarized by Martin 1992a) is 0.20 for the Kirtland's Warbler (*Dendroica kirtlandii*).

Predation appeared to be the primary cause of nest failure for Wilson's Warblers breeding in coastal riparian woodlands in Marin County. However, we documented a relatively high rate of brood parasitism and believe that the combined effects of parasitism and predation explain the poor reproductive success. For example, the difference in nestling number between parasitized and unparasitized nests was large and contributed to reduced reproductive success. Our results are similar to those of other studies in that they point to nest predation and brood parasitism as the leading causes of nesting failures in songbird populations (reviewed by Martin 1992a).

While predation and parasitism were high at all study sites, they were significantly greater at Muir Beach than at the other sites. Although our sample size of nests at Muir Beach was low, we suspect that the higher levels of predation and parasitism at that site may have resulted from the nests' close proximity to a public picnic area, a horse stable, and a small residential community. Predator densities and predation pressure are higher in areas near suburban landscapes (Wilcove 1985, Andrèn 1992). At Muir Beach, it is likely that several native and non-native predators are in greater abundance than at our other sites. For example, house cats were only observed at Muir Beach, and several corvid species frequent the picnic area and, perhaps, the nearby bird feeders. Additionally, raccoons (*Procyon lotor*) may have been more abundant at Muir beach, as they are commonly known to forage from trash cans. In addition, cowbirds may have benefited from the horse pasture, feeders, and mowed picnic area at Muir Beach.

We observed significantly lower reproductive success in warbler nests parasitized by cowbirds. Clutch sizes in parasitized nests were smaller, probably the result of egg-removal behavior by female cowbirds, as were hatching and fledging success. In general, parasitized nests failed entirely. We observed only one instance of warbler young fledging from a parasitized nest.

Brown-headed Cowbirds experienced poor reproductive success in Wilson's Warbler nests due to high rates of nest predation; cowbird fledging success was notably lower than that reported for several other species of cowbird hosts (reviewed by Ortega 1998), suggesting that warblers in this region may not be optimal cowbird hosts.

The Wilson's Warbler is considered an uncommon cowbird host (Ammon and Gilbert 1999), yet it was one of the most common host species at our study sites (Point Reyes Bird Observatory unpubl. data). The proportion of nests parasitized in our study (33%), together with estimates for Santa Barbara and San Luis Obispo counties, California (55%, $n = 11$; Friedmann et al. 1977), suggest that Wilson's Warbler is a common cowbird host in coastal California.

High levels of nest predation combined with brood parasitism are adversely affecting this population of Wilson's Warbler. Based on our demographic population model, this local population constitutes a sink; efforts to identify source populations within the region are needed to determine whether the regional population can be sustained. High levels of nest predation combined with the effects of brood parasitism point to the underlying causes of recent population declines. Low reproductive success appears to be associated with the proximity of nesting sites to human habitation (i.e., our Muir Beach site), although success was poor at all of our sites. Nest-monitoring data from other sites in coastal California are needed to understand the metapopulation dynamics of this species. Wilson's Warblers are not restricted to riparian habitats in coastal Marin County and studies that compare reproductive success among different habitats (e.g., riparian versus coniferous forest) would be useful.

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